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REVIEW ARTICLE

REGULATION AND CONTROL OF POTATO TUBER DORMANCY AND SPROUTING

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ABSTRACT

Potato crop is one of the most important vegetable crops. Potato tubers are the economic part used in human nutrition and at the same time the part used for multiplying. Tubers enter obligatory dormancy when they mature. The dormancy of tubers comprises a wide range of physiological and biochemical processes. The status and duration of dormancy depend on the genetic background, tuber's development stage, environmental conditions and operations during tuber's growth and storage. Abscisic acid and ethylene maintain the dormancy of the tuber. While gibberellins, cytokines, and indole acetic acid stimulate sprouting of tubers. Most studies on the dormancy of the tubers and the sprouting are very old and do not explain the mechanisms of dormancy regulation. Accordingly, we conducted this study with the aim of clarifying the mechanism of regulating the dormancy of potato tubers. Note:In this article we have relied mainly on some articles, (specially: CIP, 1989; Aksenova *et al.,* 2013; Muthoni *et al.,* 2014), which are mentioned in the references. So that they are linked, reformulated and developed in order to enrich the subject, which is of utmost importance to both farmers and researchers alike, and we hope that we have succeeded in reaching the desired goal.

INTRODUCTION

Solanum tuberosum L. is one of the most important and widespread vegetable crops. The world's fourth-largest food crop after wheat, rice and maize. Potato is ranking first in the volume of production between root crops and tubers. Its annual production is about 380 million tons planted on 20 million hectares. Potatoes are grown in more than 150 countries around the world from latitude 65º north to latitude 50º south, from sea level to a height of 4000 m above sea level. The average potato production in the world is 20 T/ha, while the average annual per capita consumption of potatoes is 31.3 kg/person/year. Europe and Asia are the principal potato producing areas in the world, accounting for more than 80% of global production, while Africa produces the lowest, accounting for about 5%. North America is the leader in terms of yield of more than 40 T/ha, followed by Europe 17.4 T/ha. While Africa comes in the last list of about 10 T/ha. In Syria, the area planted with potatoes is 30 thousand hectares and productivity is estimated at 540thousand tons (equivalent to 18 T/ha), (FAO, 2014). Potatoes are cultivated for their tubers, which consume cooked or processed. It is rich in nutrients and contains 25% dry matter consisting of starch and proteins. Potato tubers also contain many of vitamins, notably vitamin C. Potatoes contain mineral salts more than other vegetable crops, which are characterized by alkaline interaction, that increases their importance. Potatoes also contain some organic acids. Starch is extracted from potato tubers and is used in the manufacture of foods, paper, adhesives and textiles. Tubers are also used in some countries to feed animals either directly or after drying or turning them into silage (Olabi and Al-Waree, 1997; Jallul and Samra, 2004).

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According to the FAO, 50-60% of the world's potato production is used for direct human food, 25% as animal feed, 10% for seeds and the remainder is used in the preparation of industrial products or disposed of as waste (FAO, 2008). Potatoes multiply in two ways: The first is sexual reproduction (True Potato Seeds). This method is used for scientific purposes and for plant breeding in order to produce new varieties. In the 1970s, efforts were made to produce potatoes through the cultivation of TPS. However, this method has not yet been applied commercially, despite its importance to countries whose environmental conditions are not conducive to the production of viral-free tubers. The second method of potato propagation is Asexual reproduction (vegetative propagation), where potatoes cultivate in complete or fragmented tubers (Olabi and Al-Waree, 1997; Homedan and Zedan, 2004). Potato tubers enter after maturity, in dormancy (or rest period). The tuber sprouts are not able to germinate even if they have suitable conditions for germination such as moisture and heat. The dormancy duration is usually six to ten weeks, Its varies according to species. Some species have the ability to germinate directly before harvest and others have the ability to germinate after harvest with a short duration while others have a long rest period. The dormancy period also varies according to the maturity and size of the tubers. Whenever tuber maturity is greater at harvest, the rest period is shorter. Moreover, larger tubers germinate faster than small tubers. The environmental conditions pre-harvest affect the dormancy period, and storage conditions also greatly affect the dormancy of potato tubers (Al-Ayyubi and Al-Muhammad, 1997; Al-Obeid and Al-Shtewi, 2004). Potatoes dormancy is one of the problems that affect the production of potato crop significantly and reflected on productivity and may cause significant losses to farmers and thus harm the economy of the country. Therefore, it is necessary to understand this phenomenon well and control it in right ways and at the right

times, reducing the negative effects on the production of potato crop. Previous studies have not been able to explain the mechanism of dormancy accurately, and clarify the impact of external and internal factors in it. In this review, we will highlight the phenomenon of potato dormancy, the internal and external factors affecting it, the methods used to control it, and the future prospects for regulating this phenomenon.

Potato tubers dormancy

Dormancy in plants is the temporary interruption of the growth of any part containing a meristem (Lang *et al.,* 1987). Plant dormancy has also been separated into three types: ecodormancy, endodormancy and paradormancy. In the ecodormancy, the growth of meristem is stopped by external environmental factors. In the endodormancy, the growth of the meristem is inhibited by physiological factors from within the same plant organ. While in the paradormancy, the growth of meristem is blocked by external physiological factors (Suttle, 2007). These terms were developed for the dormancy of plant buds (Chao *et al.,* 2007), but also used for dormancy of potato tubers. During their life cycle, potato tubers can display all three sorts of dormancy (Suttle, 2007). In potatoes, dormancy is the physiological state of tuber, in which no sprouting will happen within 15 days, even when the tuber is conserved in ideal conditions for growth (Ittersum, 1992; Struik and Wiersema, 1999). During this period, post-harvest environmental conditions have only limited effect on the behavior of sprouts. Therefore, this period is assorted as an endodormancy period, and its length depends to large extent on the variety and to some extent on ecological conditions during tuber growth (Davidson, 1958; Wurr and Allen, 1976; Burton, 1978).During dormancy, biochemical and physiological processes occur but do not lead to direct morphological changes, although these processes are related to the number of sprouts produced after the break of the dormancy stage and the growth force of the tuber (Aksenova *et al.,* 2013; Muthoni *et al.,* 2014). After the maturing of the tubers and when its reach their final sizes, they enter into deep internal dormancy. During the winter, tubers remain dormant to protect themselves as vegetable reproduction organs under conditions that are unfavorable to growth. During the dormant period, the tubers are very resistant to pathogens, thus maintain their starch and protein reserves for future germination (Ozeretskovskaya, 1990; Sukhova and Korableva, 1990). In general, tuber dormancyis an adaptation of the potato plant to allow successful propagation of its species (Suttle, 2007). After the dormant period, the tuber's eyes wake up and the sprouts begin to grow intensively and form roots in their bases. At this time, tubers are transformed from a storage organ to a source of food and energy to secure the growth of sprouts. Here the vegetative propagation cycle is completed, and a young plant, a new generation of the native plant, is established (Struik, 2007). Post-harvest dormancy is used for applied objectives and is defined as the period from the elimination of aerial parts to the time when 80% of tubers display sprouts not less than 2 mm in long (Van Ittersum and Scholte, 1992).Studies have revealed that the post-harvest dormancy period is longer for small tubers (newer) than big tubers (older) (Suttle, 2007). During the development of the tubers on the plant, the sprouts progressively become dormant, starting with the end of the stolon. The apical eye is the last to enter into dormancy (Van Ittersum, 1992). A decline in late dormancy in the growth season was observed with a slowdown in the formation of the tuber mass. Separation of tubers from plants, either as a result of natural aging or the removal of mechanical or chemical plants, enhances the dormancy of the tuber during the weeks following the removal process. The force of dormancy in stored tubers decreases with time, and at the end of the storage period, the ability of sprouts to germinate improves. The duration of dormancy also depends on soil and environmental conditions during development, tuber maturity at harvest, storage conditions, and tubers infection with pathogens (Ezekiel and Singh, 2003). Therefore the understanding of factors responsible for the dormancy of the tubers and their control is important for both potato tubers designated for seeds and table. This study comes to illuminate the mechanism of regulating the potato tubers dormancy and prospects of control.

Regulation of dormancy

Dormancy is a complex process that depends on the genetic background, tuber's evolution, environmental conditions and service processes during tuber growth, storage conditions, exposure to internal and applied dormancy break compounds, and tuber injury caused by harvest, diseases and pests. The genetic factor is the most important of all these factors (Aksenova *et al.,* 2013; Muthoni *et al.,* 2014).

Genetic factors: Previous studies have shown that the genetic mechanisms of dormancy are very complex. QTL analysis showed that tuber dormancy is a quantitative hereditary character (Kotch *et al.,* 1992) and is controlled by at least nine distinct chromosome sites (Ewing, 1995; van den Berg *et al.,* 1996). Freyre *et al.* (1994) and van den Berg *et al.* (1996) have shown that six genes and nine genes, respectively, affect the dormancy of the tuber either alone or through overlapping interactions between them. Given the genetic complexity of the control of dormancy, physiological processes that regulate the progression of dormancy are likely to be complex. There is a very extensive range of dormancy period length in cultivated and wild species potatoes. It was observed that wild potato groups are characterized by long tuber's dormancy in general, whereas the reverse is often true in potato strains developed through recent breeding programs (Suttle, 2007). The exclusion to this rule is the *Solanum phureja* group, which is characterized by a very minorsize and long dormancy of potato tubers (Huamân and Spooner, 2002). In contrast, *Solanum jamesii* tubers, a wild type close to potatoes native to Arizona and New Mexico, may remain in dormancy 8 years at 4°C, while still maintaining the ability to germinate naturally when exposed to appropriate temperature (Bamberg, 2010). Simmonds (1964) showed that there was a strong correlation between the dormancy of the true potato seeds and the dormancy of the tubers. It also proved that the dormant inheritance of both seeds and tubers in the potato was multi-genetic and shared by at least three genes. TPS have a longer dormancy period than tubers and can last for four to nine months. Subsequently dormancy is associated with species, it is possible to breed late ripening species with relatively short dormancy and early ripening species with relatively long dormancy (Beukema and van der Zaag, 1979). Commonly, late-maturing breeds have a longer dormancy and more difficult to break than early-ripening breeds (CIP, 1989).

Environmental factors: Environmental conditions during growth affect the dormancy of the tuber for many species, and may result in some differences depending on the location of the crop. Temperature, humidity and photolysis during growth and storage are important environmental factors governing the

behavior of sprouts (Uwe, 2001). High temperatures, low soil moisture and reduced soil fertility during tuber growth accelerate physiological development and reduce the dormancy duration (CIP, 1985). The storage of tubers at high temperature and high relative humidity, as well as changing atmospheric composition, promotes the break-up of dormancy and growth of early sprouts (Aksenova *et al.,* 2013). Volatility of storage temperatures also shortens the dormancy period more than constant temperature rise (Muthoni *et al.,* 2014). Both pre- and post-harvest factors can affect the period of dormancy. Among the environmental conditions affecting the tubers dormancy, temperature appears to be most influential (Turnbull and Hanke, 1985a).

Temperatures during plant development: Warm or Cold weather during the growth of tubers in the field usually leads to short or long dormancy, respectively. Warm years are often associated with shorter dormancy and cold years with longer dormancy. However, warm temperatures at the time of vegetation removal can have a significant influence on physiological age in general and on dormancy in particular. Dormancy is lost more quickly when temperatures are warm shortly before or after harvest, with the largest drop in dormancy at temperatures above 50 ºC (Burton, 1989). Depending on the potato variety, high field temperatures (above 35 ºC) can lead to the immediate termination of tuber's dormancy and to a physiological disorder known as heat germination (Suttle, 2007). The dormancy of the tubers is restored if the field temperature returns to moderation. The significant effect of this condition and the restoration of dormancy are caused by deformation and complexity of tubers with low starch content, high sugar levels and poor quality (Suttle, 2007). Temperature fluctuations between night and day affect the dormancy of the tubers, and the large variation in daily temperatures has been shown to accelerate the loss of tuber's dormancy (Muthoni *et al.,* 2014).

Temperatures during storage: Storage temperature has a remarkable effect on the length of dormancy. Where the high storage temperature accelerates physiological aging processes in the tubers and thus reduces the dormancy period. There is confirmation that coldness (1-3 ºC) shortens dormancy in some varieties that have long dormancy periods (Wurr and Allen, 1976; Harkett, 1981). Davidson (1958) and Burton (1978) note that raising the storage temperature (about 30 ºC) can end dormancy before maturity. The length of dormancy is proportional to storage temperatures between 3-25 ºC (Burton, 1989). The tubers kept at temperatures of 3 ºC or less will not sprout regardless of the state of physiological dormancy and are in an endodormancy. The dormancy is suddenly broken and sprouts beginto germinate when returning to moderate temperatures if prolonged exposure to temperatures is less than 2 ºC or higher than 30 ºC (Wurr and Allen, 1976). Unstable storage conditions between high and low temperatures have been revealed to break dormancy in seed tubers (Burton, 1963). Wurr and Allen (1976) found that storage for 14 days at 2.8 ºC augmented the growth rate of sprouts when tubers were returned to 15.6 ºC and broken dormancy in tubers kept at 10 ºC. Thomas and Wurr (1976) also indicated that tubers deposited at 20 ºC for 14 days and 15 ºC contained a greater amount of gibberellins and a lower growth inhibitor than those stored at 15 ºC. It has been shown that increased germination rate is observed after a period of storage temperature reduction. Because storage temperature fluctuations result in a shortening of the dormancy period more than constant temperature rise, storage temperatures should be kept as stable as possible in order to delay the growth of sprouts. Although cold temperatures during storage can only prolong the dormancy period, they generally lead to increased sugar content, especially glucose, which is undesirable in manufacturing processes due to blackout of the fried products. So low storage temperature is not suitable for the potato intended for marketing. On the other hand, observablesprouts on potatoes are unacceptable to consumers(Muthoni *et al.,* 2014).

Storage gas phase: The structure of the storage gas phase has miniature effect on the dormancy of the tuber, provided that extreme conditions are avoided (Suttle, 2007). All hypoxia leads to temporary anaerobic life in the tuber that can break the dormancy stage (Burton, 1989). It is known that temporary anaerobic life (about one week) or partial will break the dormancy phase regardless of the age of the tuber (Burton, 1968; Thornton, 1933; 1938; 1939; Coleman, 1987). The ability of the water to break the dormancy of the tuber at first is rapid (within 2-6 hours depending on the temperature) in anaerobic conditions (Goodwin, 1966; Burton, 1978). Thornton (1939) referred that high concentrations of CO_2 (10-60%) were more effective with 20-80% O_2 than total anaerobic life due to nitrogen. A little concentration of oxygen (less than 10%) for 10 days in existence of 10-60% CO_2 or a highCO_2 (60%)/O_2 (40%) concentrations cause dormancy breakdown unrelatedly of the variety (Coleman and McIcerney, 1997). Coleman (1998) reported that treatment of dormant tubers with concentrations of CO_2 (20%) and O_2 (40%) was very effective in ending the tubers dormancy. Conversely, a CO_2 concentration of less than 10% has no effect on the duration of dormancy per se, but stimulates sprout growth later, perhaps by inhibiting the action of ethylene (Burton, 1989). Thornton (1933) observed that tuber dormancy can be effectively broken by tubers treatment with concentrations 40-60% of CO_2 and 20% of O_2 continuously for 3-7 days at 25 °C. This effect was later demonstrated by high concentrations of O_2 (20-80%) (Thornton, 1939). The results showed that the most effective combinations to breakdown dormancy and sprouting were 20% CO_2 / 40% O_2 or 60% CO_2 / 18-20% O_2 and their effects were more enhanced using 50 ppm ethylene. Where the presence of 50 ppm ethylene with 20% CO_2 / 40% O_2 mixture was already similar to bromoetane (Coleman and McIcerney, 1997). Some of the results showed that CO_2 had a dual effect, when sprouts growth was stopped using a 15% concentration and then stimulated by using lower concentrations. Generally, the optimal concentration differs according to the tubers samples (Burton, 1958).

Photoperiod: In field conditions, it is difficult to determine the effect of the photoperiod on the dormancy of tubers (Burton, 1989). The dormancy period in tubers was considerably reduced when exposed to a photoperiod of 8 hours rather than in total obscurity during tuber initiation (Tovar *et al.,* 1985). The presence or absence of light during post-harvest storage has a minor effect on the dormancy period but seriously affects the sprouting (Suttle, 2007).

Physiological tuber age: The tuber's dormancy varies according to the varieties, due to the difference in the size of the tubers so that the smaller tubers are characterized by a longer dormancy than the larger ones. The immature tubers usually have longer dormancy after harvest than the tubers harvested at maturity. This difference in dormancy between immature and mature tubers can last up to several weeks

(Krijthe, 1958). The ability of tubers to germinate increases with age, but they return and decrease after prolonged storage (Krijthe, 1962). The process of physiological aging begins since the initiation of the tuber, and can control the rate of aging, it is slow at temperatures below 5 ºC and faster at temperatures above 25 ºC (Toosey, 1964). It was found that unripe tubers have a greater aptitude to germinate at a definite time than mature tubers stored in the same circumstances (Krijthe, 1962; Hutchingson, 1978a; Hutchingson, 1978b).

Phytohormones: Tuber dormancy is thought to be regulated by relative concentrations of stimulants and growth inhibitors (Hemberg, 1985). Plant hormones are the most important and effective internal regulators in the dormancy of the tubers and developing of their sprouts (Rappaport and Wolf, 1968; Suttle and Banowetz, 2000; Coleman *et al.,* 2001). This is evident from changes in endogenous hormones associated to the stages of dormancy, growth of sprouts, the probability of changing the dormancy period and the development of sprouts through the treatment of tubers with hormonal preparations (Hemberg, 1985; Suttle, 1996).

Abscisic acid: Abscisic acid (ABA) is one of the major hormonal regulators to enter into and maintenance dormancy. Abscisic acid was first identified in potato tubers within complex inhibitors containing also other acidic growth inhibitors such as para- and ortho-coumaric acids and derivatives of cinnamic and salicylic acids. This compound was existing in dormant tubers, but its content reduced sharply by the end of dormancy and the beginning of germination of tuber sprouts (Hemberg, 1985). It was found that the abscisic acid content in both the eyes and tissues parenchyma of the tubers increased at the onset of dormancy. The highest level during deep dormancy was severely reduced at the end of the dormancy phase (Korableva *et al.,* 1980; Suttle, 1995). The prospective role of ABA in dormancy regulation was also confirmed by observation that two (Simko *et al.,* 1997) or three of QTLs (Classens and Vreugdenhil, 2000) affect the content of ABA in tuber. The abscisic acid content in the tubers is generally high at harvest time, and reduces during post-harvest storage, which overlaps with the breaking of dormancy. Abscisic acid levels should descent below a certain threshold level before stimulation of sprout development. One study showed that there was a significant negative correlation between the growth rate of sprouts and the basic ABA levels in the tuber tissues of ten potato varieties (Coleman and King, 1984). External abscisic acid is also capable to inhibit the growth of potato sprouts when realized frequently with high concentrations (El-Antably *et al.,* 1967). ABA content in tubers decreased after forcibly breaking dormancy (Suttle, 2007). Also, ABA content in tubers can be avoided by the inhibitor of ABA (fluoridone), which induces to break premature dormancy (Suttle, 1995). Analyzes at the molecular and gene levels confirmed the important role of ABA in entering and maintaining dormancy in tubers (Simko *et al.,* 1997). The gene expression encoding enzymes of ABA biosynthesis and degradation during the whole period of tuber dormancy was achieved by qRT-PCR (Destefano-Beltran *et al.,* 2006). It has been revealed that enzymes of ABA biosynthesis 9-cis-epoxycarotenoid dioxygenase (StNCED) and catabolism ABA-8'-hydrolase (StCYP707A) play a critical role in the maintenance of necessary level of ABA. The level of StNCED gene expression was related with the content of ABA throughout dormancy in the meristem and cortex tissues. In late dormancy, StCYP707A genes are stimulated in the meristem and periderm, and this leads to a decrease in the content of ABA in these tuber zones (Suttle *et al.,* 2012).A remarkable reduction in the expression of a number of known genes prompted by the ABA was detected in the tuber sprouts. It is clear that by the end of the dormancy period, the low ABA content in the tubers is allied by a down-regulation of genes responding to ABA signaling (Campbell *et al.,* 2008).

Ethylene: Ethylene is necessary for the initiation and maintenance of ampleendodormancy of tubers (Suttle, 1998). It has been noted that the role of the endogenous ethylene in regulating the endodormancy of the tubers is uncertain, while the treatment with ethylene (or ethylene release factors) produce contradictory reactions (Suttle, 1998). The participation of ethylene is evidently confirmed in the early stages of dormancy (Korableva and Platonova, 1995; Suttle, 2004a). The level of endogenous ethylene was higher in tubers dormant and cultured *in vitro*, and then decreased rapidly. The production of ethylene from tubers cultivated in the field is the uppermost directly after harvest and then decreases to low levels (Cvikrova *et al.,* 1994). The treatment of tubers that enter into dormancy with ethylene, silver nitrate and norbornadiene, causes early sprouting, which can be stopped by the usage of ethylene. Maintenance of dormancy under the effect of ethylene was detected only in the primary period of dormancy (Suttle, 1998). Data on the role of ethylene in maintaining and breaking of dormancy are inconsistent, and the strengthening or weakening of tubers exposed to ethylene depends on the dose of ethylene, the potato variety and storage conditions (Rylski *et al.,* 1974). The temporary increase in ethylene production is likely to occur during the interruption of dormancy under the influence of wounds, the treatment of bromoethane and other methods in response to stress states (Alexopoulos *et al.,* 2008; Alexopoulos *et al.,* 2009). At the same time, the comparison of dormant or sprouting tubers showed the possibility of the participation of ethylene in preventing the growth of sprouts during the latest period of dormancy (Hartmann *et al.,* 2011). Depending on the concentration and length of treatment, exogenous ethylene either quickens or delays tuber sprouting. The relatively short treatment of ethylene (less than 3 days) terminates tubers dormancy before maturity (Alam *et al.,* 1994).Whereas long or continuous treatment with similar concentrations of ethylene prevents development of sprouts later (Rylski *et al.,* 1974). Both pre- and post-harvest treatments with ethylene-releasing agent (ethephon) have directed to important delays in the dormancy of the tuber (Cvikrova *et al.,* 1994). Similarly, it was noted that treatment with the ethylene-releasing agent, alone or in combination with gibberellin on dormant tubers, stimulated the growth of sprouts (Shashirekha and Narasimham, 1988). Some studies have shown that continuous treatment with ethylene is an effective inhibitor of sprouts growth in commercial cases, although it also led to an undesirable accumulation of reduced sugars (Prange *et al.,* 1998). Transcripts with sequences homologous to those encoding components of the ethylene signaling pathways in tomato and Arabidopsis were vigorously expressed in dormant sprouts, but their expression reduced during sprouting. The genes expression of primary and secondary response to ethylene signal was also decreased at sprouting. All of these data indicate the involvement of ethylene signaling in the maintenance of tuber sprouts dormancy (Aksenova *et al.,* 2013). There are also reports of interfering of ethylene with ABA in regulating of tuber dormancy. Treatment of dormant tubers with Ethylene producer 2-chloroethylphosphonic acid

did not only augment the content of ethylene in tissues, but also motivated ABA biosynthesis, thus prolonging the deep dormancy period (Korableva and Platonova, 1995).

Brassinosteroids: Brassinosteroids (BS) are effective plant growth regulators. The data indicate a potential effect of brassinosteroids on the levels of ethylene and abscisic acid in natural regulation of tuber dormancy, and there may be synthetic elimination of sprouting by high concentrations of brassinosteroids. Korvelva *et al.* (2002) treated potato cv. Nevskii tubers, which were in post-harvest dormancy, with 24-epiprasinolide.This treatment prolonged the dormancy of the tubers and delayed of their sprouting for more than a month and enhanced the formation of ethylene and the accumulation of free and bound ABA in tuber sprouts. In addition, electronic microscopic observations displayed that delayed eye development under the effect of brassinosteroids was associated with a reduction in cell sizes in the central part of the meristem with an increase in the number and decrease in the size of vacuoles in meristematic cells (Korbleva *et al.,* 2002; Platonova and Korableva, 1994).

Auxins: Auxins, indole acetic acid (IAA) mainly, is one of the plant hormones that stimulate plant development. The treatment of dormant tubers with IAA did not show a specific influence. High concentrations of endogenous IAA or artificial auxins prevented the growth of eyes slightly, while low concentrations stimulated the growth of sprouts slightly (Suttle, 2007; Hemberg, 1985). An analysis of the content of IAA throughout the dormancy period gave unclear results. The first studies also showed that the auxins content was lower in early dormancy, then gradually increased and achieved the highest level during the growth of active sprouts (Sorce *et al.,* 2000; Suttle, 2007). Sorce *et al.* (2009) found the uppermost content of free and bound forms of IAA (esters, amides) in tuber buds during the early period of deep dormancy and considerably reduced at its end. The histochemical analysis of the distribution of IAA in the tuber tissue and sprouts led to the assumption that this aux in stimulates the completion of dormancy and accelerates the differentiation and growth of the bud at early sprouting (Sorce *et al.,* 2009). Bioinformatics data showed that the endogenous levels of IAA were low in dormant tubers and augmented during the primary growth of buds (Hemberg, 1949). Exogenous auxins such as IAA and NAA are strong inhibitors of growth of sprouts at relatively high doses (Denny, 1945). Although very low concentrations of auxins motivated the growth of non-dormant sprouts, but had no evident effects on the dormant eyes (Hemberg, 1949). Since then, there has been no report that the exogenous IAA (or any other auxins) dismisses the tuber's dormancy before maturity (Suttle, 2004b). The subsequent data did not support the role of endogenous IAA in adjusting the dormancy of tubers. The researchers suggested that IAA (or other endogenous auxins) had a role in the growth of the sprouts later (Suttle, 2004b). This suggestion is in agreement with the results of Faivre-Rampant *et al.* (2004), who isolated from sprouting potato cv. Desiree tuber transcripts encoding a protein factor alike (78% identity) to the auxin responsive ARF6 factor of arabidopsis. These copies were totally absent in the eyes and tissues of dormant tubers, but their level amplified considerably at the beginning of development of buds. The transcriptional analysis of buds of sprouting potato tubers cv. Solara indicated that the level of transcripts encoding enzymes relatedtoauxin biosynthesis, aldehyde oxygenase and flavinmonoxidase, has improved during the early stages of sprouting. Important activation of several principal auxin response genes and genes for PIN1-like auxin transporters was also detected (Hartmann *et al.,* 2011). The above findings support the idea of auxin involvement in the initiation of growth of the tuber bud and subsequent growth. Therefore, these results were very expectable, since the active participation of IAA in plant growth and differentiation processes is well identified. However, it is still unclear whether auxins play any more specialized role in controlling the initiation, maintenance and termination of tubers dormancy (Aksenova *et al.,* 2013).

Jasmonates: Jasmonic acid (JA) and its derivatives (tuberonic acid and others) are composites that motivate the formation of tubers in potato explants grown *in vitro* (Yoshihara *et al.,* 1989). However, to date there is no definite confirmation for the participation of these compounds in regulating the dormancy of potato tubers and their sprouting. Data attained by researchers on changes in JA content during dormancy and sprouting seem to be inconsistent. It was reported that the content of jasmonates changed in different potato parts during the vegetation period and achieved the highest level of tubers prior to the onset of deep dormancy (Abdala *et al.,* 2002). Suttle *et al.* (2011) directed a detailed analysis of JA and its derivatives on minitubers of potato cv. Russet Burbank and discs cut from these tubers containing the periderm and apical bud. The content of the JAstayed low in the discs of dormant tubers and improved with the development of the sprout and then reduced again. The content of tuberonic acid was high through the dormancy of the tubers and also augmented during dormancy progression, while the level of jasmonoyl-isoleucine was very movable and varied significantly from year to year. The effects of tubers treatment with JA are also ambiguous. In some experiments, the treatment of kept tubers stopped the development of the sprouts (Abdala *et al.,* 2002). In other cases, JA was stopped or motivated tuber sprouting depending on the concentration used (Platonova *et al.,* 2010). It was also described that the treatment with JA caused diverse responses from tuber sprouts when using different experimental models. As it did not affect sprouting of all potato minitubers but inhibited the development of 29% of cut tubers (Suttle *et al.,* 2011). There have been reports that the treatment of JAconsiderably affected some structural features of the cells in apical meristems of dormant tuber buds (at 4°C) and through their growth (Platonova *et al.,* 2010). The JA has altered the ultrastructure of the plasmalemma and the plastid apparatus of eye meristematic cells and its influence was better with the existence of other hormonal composites, particularly salicylic acid (Platonova *et al.,* 2010; Ladyzhenskaya and Korablyova, 2011).

Cytokinins: Cytokinins (CK) are effective regulators for the dormancy of tubers and their sprouting. It facilitates the transition from the dormancy of the tuber to breaking it and sprouting. Several analyzes of the activity and content of cytokinins showed that during deep dormancy the content of cytokinins in the tubers is low and then increases and reaches the maximum level before sprouting (Hemberg, 1985; Turnbull and Hanke, 1985b; Suchova *et al.,* 1993). Sutle and Banowetz (2000) have revealed that when the dormancy is broken, the entire content of cytokinins in tubers and sprouts, containing*cis*- and *trans*-zeatin and cytokinins of the isopentenyl type. Suttle (1998) concluded that the application of cytokininresulted in the expiry of dormancy and the reinforcement of sprouting of potato tuber .There seems to be a

different sensitivity to exogenous cytokinins by tubers depending on the precise stage in the tuber dormancy period. Exogenous cytokinins were effective in breaking dormancy only during short periods immediately after the onset of dormancy and immediately before its end (Turnbull and Hanke, 1985a). The influence of exogenous cytokinins and modifications in zeatin-like endogenous cytokinins support the opinion that the changes in both hormone levels and tissue responses of cytokinins play essential roles in the control of dormancy (Turnbull and Hanke, 1985a; Turnbull and Hanke, 1985b). Treatment of dormant tubers with various natural and synthetic cytokinins, especially benzyl adenine (BA), leads to breaking of dormancy and initiation of sprouting (Hemberg, 1985; Suttle, 2007). It was found that dormancy of tubers was effectively broken with benzyl adenine at a concentration of 20 ppm and used for 24 hours (Suttle, 2004b).

The synthetic CK, derivatives of phenylurea or nitroguanidine, were found to be more efficient in breaking the dormancy of the cv. Russet Burbank than the natural zeatin (Suttle, 2008). This may be associated with greater resistance than synthetic CK to enzymatic degradation. An essential role of endogenous cytokininsin activation for prolonging tuber dormancy period was definite on potato plants transformed with an arabidopsis gene encoding one of the key enzymes responsible for CK inactivation, cytokinin oxidase/dehydrogenase (Hartmann *et al.,* 2011). The expression of this gene delayed the onset of sprout growth from 5-8 weeks. The treatment of tubers with benzyl adenine restored the normal timing of sprouting. Improved CK biosynthesis under the effect of the agrobacterial *ipt* gene has also reduced the dormancy period in the discs cut tubers of transformed potato (Hartmann *et al.,* 2011). Suttle (2001) also found that the tubersensitivity toCK changed during dormancy progression. Tubers did not respond by weakening the dormancy by treating with *c is*- or *trans*-zeatin directly after harvest, but during storage, the sensitivity to plant phytohormones augmented in a time-dependent manner, and the dormancy was terminated by treatment with CK. This increase in the sensitivity of tuberto CK was not related with modifications in zeatin metabolism but was obviously associated with the activation of CK. Hemberg (1970) displayed that both natural and synthetic CK could break the tuber dormancy. The increase in the content of CK is the main factor leading to the breakdown of the dormancy stage in tubers (Turnbull and Hanke, 1985a; Suttle, 2004b), but may not control following growth of sprouts (Turnbull and Hanke, 1985a). Data achieved shows the participation of various CK forms and their biosynthesis and inactivation processes in the regulation of tuber dormancy and sprouting. CK realizea number of functions in plants, specially, stimulate cell division and increase tissue sink capacity (Romanov, 2009). It is believed that the role of CK in the break of dormancy is primarily related to the stimulation of cell division by allowing the transition to the stage of G1/S in the cell life cycle at the end of dormancy. The removal of this constraint is believed to occur by involving of D-type cyclins (Chao *et al.,* 2007). In addition, breaking the dormancy of sprouts transforms them into active reservoirs of storage metabolism results from other parts of the tuber. Therefore, the role of CK in increasing the bud sink capacity is also probable, and does not rule out the consequence of other pathways of CK regulation of tuber dormancy and sprouting (Muthoni *et al.,* 2014).

Gibberellins: Gibberellins (GA) are thought to stimulate the growth of active sprouts after breaking the tuber dormancy. According to previous studies by Hemberg (1985), GA promote the break of dormancy and the initiation of growth of sprouts. These trialsindicated that the activity of endogenous GA-like composites is low during dormancy and increases before sprouts grow. In storage of tubers, they can be broken by treatment with GA. Rappaport *et al.* (1958) identified that the nodes are the sites of the synthesis of GA and CK, and that tubers are usually broken with exogenous GA. GA_3 are frequently used in seed certification programs where rapid re-planting of seed tubers is necessary to test for pathogens. The data indicate that endogenous GA do not closely involved in the control of dormancy, but play a main role in later elongation of the sprouts (Suttle, 2004a). The treatment of dormant tubers with GA was used in practical applications as a commercial method of early potato planting (Claassens and Vreugdenhil, 2000). At the same time, subsequent studies did not provide a clear confirmation of the involvement of endogenous GA in breaking of tuber dormancy, but rather their role in stimulating the growth of sprouts (Suttle, 2007). Thus, the dormancy period and control of sprouting were similar in mutations of dwarf potatoes and normal phenotype plants, although there was no significant activity of GA_1 and GA_{20} in mutations (Suttle, 2004a). The artificial reduction in endogenous GA_{20} and GA_1 content by the antisense expression of the GA biosynthesis gene *GA20ox1* did not significantly affect the dormancy period but delayed growth of sprout later (Carrera *et al.,* 2000). Similar results were attained on transformed potato plants with enriched expression of *GA20ox1* gene related with GA_1inactivation (Kloosterman *et al.,* 2007). However, other reports from Viola *et al.* (2001) and Hartmann *et al.* (2011) propose the possibility of breaking of dormancy associated with GA, stimulating bud outgrowth, and encouraging growth of sprout later.

Phytohormone Interaction: Recent studies on the regulation of plant hormones have revealed complex interactions between different plant hormones, observed at the level of both physiological responses and hormonal signals (Ross *et al.,* 2011). The interaction between different plant hormones was also observed in regulating the dormancy and sprouting of potato tubers. Some investigators have presented a close interaction between GA and CK in regulation of tuber sprouting. Consequently, slight tubers dormancy of potato plants resulting from TPS was broken more quickly after treatment with a combination of GA and benzyl adenine from the treatment with these compounds separately (Alexopoulos *et al.,* 2007). Transgenic tubers, characterized by a sharp reduction in the activity of endogenous CK under the influence of a gene that encodes cytokinin oxidase / dehydrogenase for GA treatment, cannot respond. The effect of GA on the prevention of growth of sprouts was eliminated by the treatment of tuber with CK and especially benzyl adenine (Hartmann *et al.,* 2011). The interaction between ABA and ethylene was detected in retaining of tuber dormancy (Korableva and Platonova, 1995). The contents of the ethylene were reduced during the sprout dormancy phase, and in parallel the activity of the IAA increased (Hartmann *et al.,* 2011). The investigation of the hormonal regulation of tuber dormancy and its break-up indicated involvement in these processes by a complex group of plant hormones, each of which performs its specific function. Interaction between different hormonal groups is coordinated in a timely manner (Aksenova *et al.,* 2013). The following table shows the complex involvement of phytohormones in regulating the tubers dormancy.

Table 1. Hormonal regulation of tuber dormancy and sprouting (Aksenova *et al.*, 2013)

Physiological processes		Phases of tuber dormancy and sprouting: stimulating phytohormones		
		Dormancy: ABA, ethylene, BS?	Sprouting: IAA, CK, GA	Sprout growth: CK, GA
Buds	Growth characteristics	Growth arrest; blocking G1/S-phase transition	Onset of growth and morphogenesis; removal of blocking G1/S-phase transition	Active growth
	Metabolism specific features	Low level of metabolism; limited supply with substrates	Activation of metabolism; enhanced supply with substrates	High level of metabolism; active supply with substrates
Tuber tissues	Growth characteristics	Absence of growth and morphogenesis	Absence of growth and morphogenesis	Absence of growth and morphogenesis
	Metabolism specific features	Low level of metabolism; preservation of storage carbohydrates and patatins	Transition from storage to source function; enhanced activity of carbohydrate metabolism	Active supply of seedlings with energetic and structural materials

Sprouting behavior

At the completion of the dormancy period, the bud in the eyes start to grow and form a minor sprout. The apical eye commences to give a sprout first announcing the commencement of apical dominance stage. Cultivation of seed tubers with apical dominance is often given to plants with single stems, and hence reduced productivity (CIP, 1985). After the apical dominance stage, supplementary sprouts grow and the multiple sprouts stage starts. This is the ideal stage for the cultivation of seed tubers as it leads to multiple stems. The existence of light helps to extend the multiple sprouts phase and retain a petite and robust sprouts (Muthoni *et al.,* 2014). Apical dominance is affected by managing storage temperature and preventing sprouting of buds. Storage of the tubers at a low temperature (4°C) until the end of apical dominance stage and then increase the storage temperature (above 15°C) to motivate the sprouting will lead to the presence of multiple sprouts. In order to limit the number of sprouts, a high storage temperature (15-20°C) is maintained, which will stimulate apical dominance. Elimination of the apical bud from the tuber may encourage the formation of multiple sprouts. This leads to the development of similar sprouts on the tuber which produces a multiple stems per plant (CIP, 1985). The seed tubers enter after the multiple sprouts stage in the aging stage. old tubers should not be desproutedeven when the sprouts are long, may lose their ability to resprout or may become very fine "hair sprouts" (Muthoni *et al.,* 2014).

Breaking of potato tubers dormancy

Breaking the dormancy stage in the potato tubers by exogenous factors has useful applications such as breaking the dormancy of seed tubers for export or local use, integrating them into seed propagation programs and rapid screening of post-harvest diseases (Coleman, 1983). The technique used to break the dormancy is probable to depend on the facilities and chemicals available as well as the genetic features of the breeding material and the varieties on which the treatments will be conducted (CIP, 1989). Most of the compounds used to break the dormancy often belong to the following categories: sulfhydryls, anesthetics, respiratory inhibitors or end products of glycolysis. Some hormones (i.e., GA and bromoethane) are used to motivate the development of potato seed sprouts (Coleman, 1987; Allen *et al.,* 1992).

Thermal treatments: The known thermal treatments are high temperature, cold shock with heat. In high heat treatment tubers are reserved in a dark room at 18-25°Cuntil sprouting starts. This method works best on very early maturing cultivars or when the dormancy period is often complete. It is not recommended to isolated individuals or other breeding materials. In the treatment of cold shock with heat, this method functions best with early maturing cultivars or when the dormancy period is finished. It can be used with some breeding material for different genetic parents. Tubers are harvested and cleaned, leaving them to heal wounds and bruises, then placed at a degree of 4°Cfor two weeks or more, and then at 18-25°Cuntil sprouting. If the buds do not emerge within 2-3 weeks, the entire process is repeated or the tubers are treated with GA (CIP, 1989).

Gibberellic acid: The newly harvested tubers are cleaned and then immersed in GA_3 solution for 10-20 min. The best results were obtained at the treatment prior to wound healing and bruising. The GA accelerate sprouting for many varieties and breeding materials, when the dormancy period is close to completion. There are many different recommendations for the use of GA concentrations, which are often based on plant material and its dormancy stage. It is recommended to use solutions containing 5-10 ppm of GA to treat all types of tubers, especially those old and containing many wounds and bruises. High concentrations (not exceeding 100 ppm) can be used on newly harvested tubers. The high concentrations of the emergence of hair sprouts, with weak growth and deformed plants. Concentrations higher than 2 ppm should not be used on tubers with sprouts. Tubers must be air dried and kept at 18-25°C until sprouting occurs. The first sprout should be removed to mitigate the adverse effects of gibberellin and to eliminate the apical dominance (Doorenbos, 1958; Choundau, 1960; Bokx, 1970).

Thiourea: Tubers are soakedin 1% solution of Thiourea for one hour. If tubers do not contain wounds or bruises, one or two incisions are made on the apical end of the tuber to ensure chemical absorption. This solution can be used for several batches of tubers if they are dust free. The tubers are air dried after treatment and stored at 18-25°C. This treatment can be used in combination with other methods but should always be performed early and also requires the creation of cracks in the tubers. This method, although safe, is not common (CIP, 1989).

Ethylene chlorohydrins: Ethylene chlorohydrin (2-chloroethanol) is a dangerous chemical (a highly volatile gas that helps breakdown the dormancy) and must be treated very carefully. It used at concentration of 7 cm^3 of chemical per liter of water and should not be used to immerse with the cut or wounded tubers because it will rot rapidly as a result of the treatment. Clean, well-formed tubers are placed in a mesh bag and immersed in the solution until the entire surface of the tubers is wet, the tubers then are removed from the solution and placed immediately on a shelf in a tight container for two or three days. The shelves ensure that the tubers are not in contact with the excess solution that is discharged from them. Wear rubber gloves and apron while handling wet tubers. Tubers are then removed and placed in dry air at 18-25°C. This method is recommended for genetic material, especially when tubers are less than 10 g, with extreme caution when transporting this chemical (Denney and Miller, 1938).

Rindite: Rindite is a combination of three compounds, containing 7 parts of ethylene chlorohydrin (2-chloroethanol), 3 parts of ethylene dichloride (1, 2-dichloroethanol), and one part of carbon tetrachloride. Carbon tetrachloride is used to accelerate the volatilization of the mixture. Rindite is very volatile, very dangerous, and causes corrosion. Users should wear rubber gloves, shoes, apron and mask and not allow chemicals to touch the skin. Treated tubers must be healthy and free of wounds and bruises. Tubers should be placed in a sealed container with a large ventilation system. Small samples of tubers (less than 5 kg) do not need ventilation system. The tubers shall be kept for 5-7 days at a temperature of 18-20°C with high humidity and sufficient air movement to ensure wound healing, and extreme care should be taken in transporting this chemical (Thornton, 1933, 1939; Bokx, 1970; CIP, 1989).

Carbon Disulphide: Carbon Disulphide (CS_2) is a volatile liquid that evaporates rapidly. Gas is flammable and toxic. The method of application is similar to that used in the Rindite, and the recommended dose rates vary from country to another. Brazil uses 45 cm^3 of CS_2/m^3 of pot size for three days at 20-25°C, and in India 50 cm^3/ton of potatoes for two weeks. Experiments in the Netherlands using 12.5-25 cm^3/m^3 of vessel volume for three days at 20°C have yielded successful results. The use of high concentrations can result in giving hair sprouts. Tubers treated with CS_2 must be mature and well-wound (Thornton, 1933).

Bromoethane: Bromoethane (C_2H_5Br) is a flammable liquid, which can be used at 0.2 cm^3/dm^3 of pot volume on fresh harvested tubers or 0.1 cm^3 with tubers close to the end of dormancy for 24-hour at room temperature. The tubers must be mature and well-wound before treatment. Liquid bromoethane is placed in a container with wicks to help evaporate. Air circulation is needed because the formed gas is heavier than the air. After treatment, the tubers are kept at a temperature of 17-20°C until sprouting. Proper precautions should be taken because both liquid and gas can be toxic to mammals. This chemical is somewhat safer for the use and transport than rindite or ethylene chlorohydrin. It is highly flammable in the higher concentrations (Coleman, 1983; Coleman, 1984; Coleman and Coleman, 1986).

Conclusion

Dormancy and sprouting are of the most important stages of tuber development. The dormancy is a genetic characteristic in potato tubers and TPS, and the genes regulating the dormancy of tubers have not yet been identified clearly. Tubers dormancy includes a wide range of endogenous physiological and biochemical processes. Phytohormones play an important role in the dormancy and sprouting of tuber buds. ABA and ethylene maintain the dormancy of the tuber. Both GA, CK and IAA stimulate the tuber sprouting. Tubers dormancy is artificially terminated by treating them with some chemical compounds, hormones, thermal processes.Most studies on the maintenance and breaking of tubers dormancy stage are very old and do not precisely explain the mechanisms of regulation and control of this phenomenon.

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